Taxonomy and biology of Nilaparvata lugens (Hom., Delphacidae)

O. Mochida and T. Okada

Although *Nilaparvata seminula* should be reexamined, 14 determined and 2 undetermined species are known as the members of the genus *Nilaparvata*. Seven determined species, including *N. seminula* and one undetermined species, are distributed in the Oriental and Australian regions. A tentative key to six species in the two regions is given. The life cycle, overwintering, development, effect of temperatures, appearance of wing forms, reproduction, host plants, occurrence, and dispersal are discussed.

THE OUTBREAKS of *Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål) (Hom., Delphacidae) on rice have been recorded in Korea since AD 18 (Okamoto 1924) and in Japan since 697 (Suenaga and Nakatsuka 1958). *N. lugens* has been serious on rice in many tropical countries in the Orient and some Pacific islands in recent years (Mochida et al 1977). Throughout the world 14 determined and 2 undetermined species are reported as the members of the genus *Nilaparvata*. This paper reviews the taxonomy and biology of *N. lugens* and several allied species.

CLASSIFICATION, DISTRIBUTION, AND HOST PLANTS

Identification of Nilaparvata

Homoptera includes such insects as leafhoppers, cicadas, treehoppers, planthoppers, froghoppers, jumping plantlice, white-flies, mealybugs, scale insects, and aphids. Those in the Oriental and Australian regions are divided into two suborders or series : Auchenorrhyncha and Sternorrhyncha. Auchenorrhyncha has two infra-orders : Cicadomorpha and Fulgoromorpha. Fulgoromorpha includes about 15 families including Delphacidae, the largest, which encompasses more than 1,100 species. Venation of the macropterous fore wings or tegumens is characteristic of the family. The spur or calcar at the apex of the hind tibia is also characteristic. Adult members of the genus *Nilaparvata* in

CRIA-IRRI, Sukamandi, West Java, Indonesia; and Tyugoku National Agricultural Experiment Station, Hukuyama, Japan. the Oriental and Australian regions may be determined from the following key:

1. Tarsi with one or two segments; antennae lacking a terminal arista; - Tarsi with three segments; antennae short, with a terminal arista; active forms Auchenorrhyncha (2) 2. Intermediate coxae short, differing in appearance from anterior coxae, inserted near the median line; hind coxae mobile; tegulae absent - Intermediate coxae long, similar to anterior coxae; hind coxae immobile; tegulae over base of fore wing Fulgoromorpha (3) 3. Antennal flagellum segmented; ocelli not outside lateral carinae of head - Antennal flagellum not segmented; ocelli outside lateral carinae of head 4. Second segment of hind tarsus small or very small, its apex without or - Second segment of hind tarsus not very small, its apex with row of small 5. One or both claval veins granulate; apical segment of labium much - Claval veins usually not granulate; if so, the apical segment of labium 6. Anal area of hind wing reticulate Fulgoridae 7. Apical segment of labium about as long as wide Derbidae 8. Claval vein extending to apex of clavus Achilixiidae, Achilidae 9. Hind tibiae with variable spines but without a large mobile and apical spur or calcar Dictyopharidae, Cixiidae - Hind tibiae each with a large, mobile and apical spur. Delphacidae (10) 10. Several lateral spines absent on basal segment of hind tarsus

Nilaparvata and tentative key to species in the Oriental and Australian regions Genus *Nilaparvata* Distant, 1906, Fauna Brit. Ind. Rhynch. 3:473. Figure 1 shows the adult morphological characters of *N. lugens*.

According to Fennah (1969, 1973/75), the two genera *Afrokalpha* and *Nethokalpa* resemble *Nilaparvata* in size and general appearance, but are distinguishable from it by spines present on the basal segment of hind tarsus (Fig. 2). Throughout the world, 14 determined and 2 undetermined species



1. Morphological characters of *N. lugens* (adult macropterous male). ac = anteclypeus; af = apex of frons: ce = compound eye: f = fore wing or tegmen; fr = frons: g = gena; h = hind wing; m = median longitudinal carina; pc = postclypeus: pr = pronotum: ps = pterostigma: r = rostrum: s = spur; st = scutellum: t = tegula: v = vertex.



2. Spines on the basal segment of the hind tarsus of *N. lugens* (macropterous male). c = coxa; f = femur; s = spur; ta = tarsus; ti = tibia.

are known in the genus (Table 1). The genitalia are the most important character that distinguishes the species, especially styles (parameres) and aedeagi for male and lateral lobes (1st valvifers) for female adults. Okada

Species	Distribution	Main host			
N. albotristriata (Kirkaldy)	Australia, Micronesia (Guam), New	_			
	Caledonia	?			
N. angolensis Synave	Angola	?			
N. bakeri (Muir)	Japan, S. Korea, Formosa, Philippines,				
	Sri Lanka	Leersia japonica			
N. caldwelli Metcalf	Puerto Rico	?			
N. camilla Fennah	Sudan	?			
N. chaeremon Fennah	Sri Lanka	?			
<i>N. diophantus</i> Fennah	Port. Guinea, Senegal	?			
N. lugens (Stål.)	From India to Korea and Japan:				
	Pacific Is. Australia	Oryza sativa			
N. maeander Fennah	Sudan, Fr. Guinea	?			
N. muiri China	China, Japan, S. Korea	Leersia sayanuka			
N. myersi Muir	New Zealand	?			
N. nigritarsis Muir	Natal, Sudan (Abyssinia)	?			
N. seminula Melichar	C. Java (Semarang)	?			
N. wolcotti Muir et Giffard	Puerto Rico	Saccharum officinarum (?)			
N.sp. ^a	Port. Guinea	?			
N. sp. ^b	Japan, S. Korea	Leersia sayanuka			

Table 1. Species belonging to the genus Nilaparvata, their distribution, and host plants.

^a Fennah (1958, p. 447). ^bNasu (1960) and Suenaga and Mochida (1966).

(1977) gave a tentative key to six species in the Oriental and Australian regions as follows :

1. Frons nearly central with an excavation intercepting median longitudina
carina (Fig.3) baker
- Frons nearly central without excavation, median carina not intercepte
2. Pronotum palish or opaque whitish; usually brachypterous
albotristriat
— Pronotum fuscous, brownish or stramineous,



3. Excavation intercepting the median longitudinal carina on the frons of *N. bakeri*.



4. Male genitalia of *N. albotristriata* (A; Kirkaldy 1907), *N. chaeremon* (B; Bb = aedeagus ventral view; Bc = the same dorsal view. Fennah 1973 75), *N. lugens* (C: Cb = aedeagus; Cc, style), *N. bakeri* (D; Db = aedeagus: Dc = style), *N. muiri* (E; Eb = aedeagus: Ec, style), and *N. myersi* (Fa = median portion of diaphragm; Fb = anal segment of male, left side; Fc = style; Fd = aedeagus ventral view; Fe = the same left side. Fennah 1965).

3. Medioventral process of male pygofer present; genital style bifurcated
apically
— Medioventral process of male pygofer absent
4. Inner margin of female lateral lobe with a spatulated process at base
(Figs. 5c and 6c) muiri
- Inner margin of female lateral lobe slightly concave near base (Fig. 6D)
sp.
5. Genital style bifurcated apically; hind tibial spur with about 20 teeth
myersi
— Genital style not bifurcated apically, hind tibial spur with about 30–36
— Genital style not bifurcated apically, hind tibial spur with about 30–36 teeth
— Genital style not bifurcated apically, hind tibial spur with about 30–36 teeth
— Genital style not bifurcated apically, hind tibial spur with about 30–36 teeth
— Genital style not bifurcated apically, hind tibial spur with about 30–36 teeth
— Genital style not bifurcated apically, hind tibial spur with about 30–36 teeth

Species distributed in the Oriental and Australian regions

• *N. lugens* (Stål, 1854) Öfv. Svensk Vet. Ak. Forh. 11:246. Synonyms include:



5. Female genitalia of N. lugens (A), N. bakeri (B), and N. muiri (C). bl = basal lamina; ll = lateral lobe.



6. Lateral lobes of *N. bakeri* (A), *N. lugens* (B), *N. muiri* (C), and *N.* sp. (D) (macropterous female) (Suenaga and Mochida 1966).

1854 Delphax lugens Stå1
1863 Delphax sordescens Motschulsky
1903 Liburnia sordescens Melichar
1906 Delphax oryzae Matsumura
1906 Kalpa aculeata Distant

- 1906 Nilaparvata greeni Distant
- 1907 Delphax ordovix Kirkaldy
- 1907 Delphax parysatis Kirkaldy
- 1907 Dicranotropis anderida Kirkaldy
- 1907 Delphacodes anderida Muir
- 1917 Delphacodes parysatis Muir
- 1917 Liburnia oryzae Matsumura
- 1932 Nilaparvata oryzae Esaki et Hashimoto
- 1935 Hikona formosana Matsumura
- 1945 Nilaparvata sordescens Kuwayama

The male has 15 chromosomes in the primary spermatocyte: n, $15 = 14_{\text{II}} + \text{X}$. The sex determination is of the XO type (Saitoh et al 1970). *N. lugens* is the only pest on rice of economic importance among the members of the genus *Nilaparvata*. The species belonging to *Nilaparvata* collected on lowland rice plants in Indonesia was only *N. lugens*. On the other hand, the light trap occasionally catches a small number of other species such as *N. bakeri* and *N. muiri* in Japan, especially in May, June, and July (Hasegawa 1955a; Nasu 1965).

N. lugens is found in India, Sri Lanka, Bangladesh, Cambodia, Thailand, Vietnam, China, Malaysia including Sarawak, Korea, Japan, Indonesia, Philippines, Australia (Queensland), Caroline and Mariana Islands. Fiji, New Guinea (Papua), and Solomon Islands.

Many plants are reported as host plants, food plants, and plants that serve for oviposition. Like Mochida and Okada (1971, p. 739), we doubt that all serve those purposes in the field. Many authors used the word host plant vaguely in relation to *S. furcifera* and *N. lugens*. We consider that when *N. lugens* repeats its generations on a plant or plants under natural conditions, such plants are regarded as its host plants. Mochida and Okada consider *Oryza sativa* as the main host, but some plants such as *O. alta, O. australiensis, O. brachyantha, O. glaberrima, O. granulata, O. latifolia, O. minuta, O. nivara, O. punctata, O. perennis, Leersia* spp., and *Echinochloa* spp. may become potential host plants in the open field. Lei and Wang (1958) noted that the eggs of *N. lugens* are deposited in the tissues of *Leersia hexandra* (Linn.) Swartz and other weeds along the sides of streams, pools, and ponds in China during the winter. As *Leersia* spp. are the host plants of allied species, however, further examination is needed regarding the identification of the species on such plants.

• *N. albotristriata* (Kirkaldy 1907) Bull. Exp. Stn. Haw. Sug. Plant. Assoc. 3:154, pls. 10 (fig. 15). 14 (figs. 1–3).

1907 Delphax albotristriatus Kirkaldy

Hind tibial spur with about 16 well-developed spines. Male pygofer apically rotundate oval, the rim thickened about the anal third and produced there in a short spine. Genital styles broad. bifid apically. Length $2\frac{1}{4}$ to $2\frac{3}{4}$ mm. Brachypterous is known. For identification see Figure 4A.

N. albotristriata occurs in Australia (Queensland, Brisbane, and Bundaberg), Guam, and New Caledonia.

The host plant of this species is unknown.

• N. bakeri (Muir, 1917) Proc. Haw. Entomol. Soc. 3: 314–315 (Fig. 47), 336–337.

1917 Delphacodes bakeri Muir

Body is slightly larger and darker than *N. lugens.* Macropterous male 2.5-3.0 mm (3.7-4.2 mm, including fore wing) and female 3.3-3.5 mm long (4.4-4.6 mm, including fore wing). Brachypterous male 2.5-2.8 mm and female 2.8-3.4 mm. Frons near center with an excavation intercepting median carina (Fig. 3). Aedeagus for male and lateral lobe for female are specific (Figs. 4-6).

N. bakeri is found in Japan, South Korea, Formosa, Philippines, and Sri Lanka. Mochida and Okada (1971) reviewed references regarding hosts. Main host is *Leersia japonica* Makino.

• *N. chaeremon* Fennah, 1973/75 Entomol. Scand. Suppl. 4: 102–103, Figs. 81–89.

For identification see Figure 4B. N. chaeremon occurs in Sri Lanka. The host plant is unknown.

• N. muiri China, 1925 Ann. Mag. Natl. Hist. (9), 16:480 (Fig. 4F).

Slightly smaller than *N. lugens.* Body length of macropterous male 2.1–2.3 mm (3.3–3.6 mm including fore wing), female 2.4–2.6 mm (3.4–4.0 mm including fore wing). Brachypterous male 2.0–2.3 mm, female 2.5–2.8 mm. For identification see Figures 4 to 6.

N. muiri is present in China, Japan, and S. Korea.

Mochida and Okada (1971) reviewed references regarding hosts, food, and oviposition plants. Many plants are reported as the host, food, and oviposition plants. However, *Leersia sayanuka* Ohwi is the main host in Japan.

• N. myersi Muir, 1923 Trans. N.Z. Inst. 54: 258.

For identification see Figure 4F. N. myersi occurs in New Zealand. Its host plant is not known.

• N. seminula Melichar, 1914 Notes Leyden Mus. 36: 110-111.

Since Melichar described one male of this species very simply, no rerecord or redescription has been known. A very small, slim delphacid, dark brown in color. Both fore and hind wings hyaline, transparent without marks. Veins extremely slim and outermost one finely granulated; outer and inner apical veins forked. Hind tibiae with two spines. Length of male, including fore wing, 2.25 mm.

N. seminula occurs in Java (Semarang). Its host plants are unknown.

• N. sp. Nasu, 1960 Delphax, 2: 3-4.

An undetermined species was recorded in Kyushu and Honshu, Japan. The same species is recorded in S. Korea (Okada 1977). This species resembles *N. muiri* but is distinguishable by the following characters: genital style dark brown, relatively thicker, with large and hemispherical outer process in caudal view. Aedeagus in lateral aspect apically curved rectangularly and produced relatively longer. Inner margin of lateral lobe of female basally slightly concave (Fig. 6D).

Leersia sayanuka Ohwi is the host.

Separation of Nilaparvata spp. in the egg and nymphal stage

Nasu and Suenaga (1956a) and Suenaga and Nakatsuka (1958) showed that *N. lugens, N. bakeri*, and *N. muiri* are occasionally distinguishable from each other in the egg and older nymphal stages by the shape of the eggcap or operculum, egg size, and both color and general appearance of nymphs. Hasegawa (1955b) indicated that in the fourth instar *N. lugens* is distinguishable from *S. furcifera* and *Laodelphax striatellus* (Fallén) by the external structure of the anal segments. However, there is no report to distinguish all these allied species in the egg and nymphal stages.

BIOLOGY OF N. LUGENS

Life cycle

The eggs are usually laid as egg-groups in the tissue of the lower part of the rice plant, mainly in sheaths but also in leaf blades. But the sizes and sites of egg-groups depend upon the stages of the rice plants (Table 2). When the adult population is high, eggs are found in the upper parts of rice plants. The egg stage is about 7 to 11 days in the tropics. The nymphal stage is 10 to 15 days. The preoviposition period averages 3 or 4 days for brachypterous females and 3 to 4 days for macropterous females. Duration of each stage depends on temperature and cultivars. In the greenhouse each female lays about 100 to 200 eggs. The adults and nymphs usually stay on the lower parts of rice plants. However, when the population is very high—in Java more than 500 per hill— they are observed to swarm even on flag leaves, the uppermost internodes of panicles, and panicle axes.

The average temperatures in tropical lowlands range from about 20 to 30° C-20 to 31° at Calcutta, 25 to 31° at Bangkok, 26 to 28° at Jakarta, and 25 to 30° at Manila. The time from appearance of the adult in one generation

Tab	le 2.	. Egg-gr	oup	sizes	and	ovip	osition	sites	in	the	paddy	field	at	maturity	on	20	plants
of	rice	cultivar	Kin	maze	(Moc	hida	1964b)	-									

Oviposition site	Egg-	Eggs in a	an egg-group (no.)	Eggs		
	(no.)	Mean	(Min to max.)	Total no	% of total	
Blades						
Upper surface	176	14.5	(2 to 62)	2558	86.6	
Under surface	44	7.7	(1 to 28)	341	11.6	
Subtotal	220	13.1	()	2899		
Sheaths	6	7.8	(5 to 13)	47	1.6	
Grand total	226	13.0	(1 to 62)	2946	100.0	

		25°C	27-28°C				
Stage	Male	Female	Male	Female			
		Brachypterous Macropterous		Brachypterous	Macropterous		
Egg Nymph Preoviposition period Total	10.5 14.1 24.6	10.4 14.3 28.4 3.8 3.9		7.9 – 7.9 – 12.0 – 3.0 22.9	3.9 24.8		

Table 3. The average time (days) between *N. lugens* generations on rice seedlings at constant temperatures (Suenaga 1963; Mochida 1964a, 1970).

to that in the following generation is 28 to 32 days at 25°C constant, and 23 to 25 days at 28°C constant (Table 3). The growing duration of existing rice cultivars in the tropics ranges from 78 to 230 days (Grist 1968). Thus, *N. lugens* may be calculated to have 2 to 8 generations during one rice cropping season in tropical lowlands. In fact, *N. lugens* has five generations on a single rice crop in southern Japan (Mochida 1964a), five or six generations in the central part of China (Lei and Wang 1958), and four or five generations in Java (Mochida et al 1977).

The seasonal occurrence of *N. lugens* depends on the presence of rice plants in the tropics. In many rainfed paddy fields in Java, rice is absent during the dry season. *N. lugens* is not found so abundantly in such fields, but is found in some rice fields irrigated in the dry season (Mochida et al 1977).

Overwintering

For more than 70 years many entomologists have been trying to find S. furcifera and N. lugens in Japan during the winter but have found only a few cases at special places. Nasu (1965) studied the eggs in diapause in seven delphacids. The embryonic development in all such eggs in diapause stopped just before the blastokinesis stage in all seven species. When eggs were kept at 25°C, embryonic development started again within several days and the eggs hatched. Nasu could not find these phenomena in the eggs of N. lugens. On the other hand, Miyake and Fujiwara (1956, 1957, 1961, 1962) and Miyake (1966) reported the overwintering and diapause of N. lugens under experimental conditions in Japan. They observed that eggs destined to diapause were laid by adults or the migratory females that had been reared on the leaf sheaths of rice plants and developed after the heading stage under conditions of high nymphal densities, temperatures lower than 17°C, and a short 10-hour day. The eggs in diapause were defined as those still alive after 24 hours at -4 C. Okumura (1963) said that adults reared in rearing tubes with a short 8-hour day and 15°C produced some unhatched eggs, and that the embryonic development in such eggs was retarded in the yellow-spot stage. He did not explain why unhatched eggs were regarded as eggs in diapause. Because the descriptions of eggs in diapause in N. lugens by Miyake and his coworkers and by Okumura

are vague, future studies should be made to determine whether those eggs contain embryos in diapause or not. Takezawa (1961) indicated that a few of the eggs laid in ratoons in mid-November survived until March or April. But rice plants and their ratoons in the main islands of Japan disappear in winter or early spring. Accordingly, there are few possibilities that *N. lugens* can overwinter in the egg stage in the main islands of Japan, except in special cases in which a very few *N. lugens* overwinter as eggs and nymphs in several small, warm areas of Southern Japan in some years (Itoga et al 1956; Sameshima 1956). Most *N. lugens* appearing in the rice fields of Japan in early summer every year have migrated across the East China sea.

Development

Nasu and Suenaga (1956b) and Mochida (1970) described the embryonic development of N. lugens The egg consists of the chorion, viitelline membrane, protoplasm, nucleus, yolk, and mycetocyte. The mycetocyte seems to be covered with a thin membrane and can be distinguished easily from other egg contents as a spherical body. It is situated at the posterior end of the egg, and is about 85 or 90 μ in diameter within 4 hours after oviposition; it holds a mass of microorganisms or symbiotes. After maturation, fertilization, and cleavage have advanced within the egg, the events that lead to the formation of the embryo begin to occur at the posterior pole of the egg from the first to the second day after oviposition at 25°C-germband formation. The mycetocyte remains at the posterior pole. Near the posterior pole a slight depression occurs and develops into the mouth of the invagination about 28 to 32 hours after oviposition. This pit deepens rapidly into a slender tube or invagination, and appears in the volk. As invagination advances, the mycetocyte is situated on the top of the vagination. The invagination proceeds in such a manner that its ventral surface faces the dorsal side of the egg, and its posterior end faces the anterior pole of the egg. The mycetocyte moves subsequently toward the anterior pole with the development of invagination on the second day. The original head, thoracic, and abdominal parts are distinguishable on the third day. At the end of the fourth day and early in the fifth day (90-108 hours), the top and the tail of the invagination are bent and developed backward and forward along the dorsal and the ventral side of the egg, respectively. Simultaneously, the mycetocyte moves along the ventral side of the egg toward the posterior pole. Now the original position of the embryo has been entirely reversed, while the mycetocyte returns to the vicinity of its original position; the blastokinesis has been completed. The rudiments of the eyes appear as red spots shortly after the blastokinesis has been completed (96 to 102 hours). The egg cap is detached from the chorion at the anterior pole of the egg on the seventh day. Hatchlings appear about 9 or 10 days after oviposition.

N. lugens has five nymphal stadia, which are distinguished by shapes of the mesonotum and metanotum, and body size (Fig. 7). Like the embryonic



7. First to fifth instars of N. lugens. ms = mesonotum; mt = metanotum.

development, postembryonic development is influenced considerably by temperature.

Effect of temperature

Table 4 shows some bionomical characters related to temperature.

Egg and nymphal stage Nymphal body fluid freezes or becomes supercooled at -6.2°C. Embryonic development ceases below 10°C according to Hirano (1942), 10.5°C according to Kuwahara et al (1956), or 10.8°C according to Suenaga (1963). Cessation of postembryonic development is set at 10.5, 9.1 or 9.8°C by the same authors. The hatchability is highest (91.5%) at about 25°C (Fig. 8). The nymphal survival rate is highest (about 96 to 98%) at about 25°C constant (Fig. 9). The time required for completion of embryonic and postembryonic development depends to a considerable extent upon temperature. The duration of the egg stage is 26.7, 15.2, 8.2, 7.9, or 8.5 days at 15, 20, 25, 28, or 29°C constant (Fig. 10), respectively. It is shortest at about 28°C. The duration of the nymphal stage is about 18.2, 13.2, 12.6, 13.1, 17.0, or 18.2 days at 20, 25, 29, 31, 33, or 35°C constant (Fig. 11), respectively. It is shortest, 12.0 days at 27°C. Thus, the shortest total span from egg to adult is about 20 days at 27 to 28°C constant when susceptible cultivars are given as foods. The temperature to which the nymph is exposed is known to affect the adult female's longevity and oviposition (Mochida 1964a). Fourth- and fifth-instar nymphs are normally active between 12 and 31°C (Suenaga 1963).

Adults. The temperature range for normal behavior is 9 to 30°C in the macropterous male and 10 to 32°C in the macropterous female (Suenaga 1963).

		25°	C constant		Natural temp.					
	B♂	M♂	B ♀	M ♀	B♂	Mð	B Q	M		
Egg Hatchability (%) Egg stage length (days) Av. Min. to max.	1	91.5 ⁴	•10.4	4 6	L	6 6	-36 ^c			
Nymph Survival rate (%) Nymphal life (days) Av. Min. to max.		14.1 (11–16)	96–98* 14.3 <i>*</i> (13–15)		L L	1 1	- 9 [¢]			
Adult					L	1	12.2 "			
Av. longevity (days)		11.6	22.3	27.6 <i>^b</i> 18.6 ^g	33.5	36.6	26.1	30.7′		
Preoviposition period (days) Av.			3.8	7.2*			2.0	0.76		
Av. (minmax.) oviposition			20.7	21.4 *			3-6 11-39	3-7° 6-42°		
Eggs/female (no.) Av.			300.7	249.0 ^{<i>b</i>}			201.6	196.2°		
Min. to max.			(86–576)	(0–812) ^b			405.7 598.5 163.7	236.4 ^h 543.1 ^h 148.5 ⁱ		
Max. Eggs/egg-group (no.)			1.74	1.77 <i>i</i>			108.2	1474 ^a 1–20 ^a 1–27 ^g		
Sex ratio	L	_1		-1				1-62*		

Table 4. Bionomical	characters of	brachypterous	(B) an	d macropterous	(M)	Ν.	lugens	kept
on rice seedlings.							-	

^aSuenaga (1963). ^bMochida (1970). ^cFukuda (1934). ^dEsaki and Sameshima (1937). ^eSoejitno et al (1974). ^rKisimoto (1957). ^gBae and Pathak (1970). ⁿKuwahara et al (1956). ^rMochida (1964a). ^rMochida (1964b).

Adult longevity is curtailed as temperature rises in a range between 20 and 33°C (Mochida 1964a). The number of eggs laid by a female is highly correlated to her life span (Kisimoto 1957) and her oviposition period (Mochida 1964a, 1970b). The oviposition rate (eggs per day per female) rises with temperature. The preoviposition period in macropterous females becomes shorter as the temperature rises in the range between 20 and 33°C; that in brachypterous females remains unchanged (Fig. 12).

To study the effect on oviposition, short exposures to different temperatures during the early adult stage of four groups of macropterous females were compared :

1. Females were kept at 28°C continuously after emergence.

2. Females were kept at 28°C for 48 hours after emergence, then permitted to oviposit at 20°C constant.



8. Hatchability of *N. lugens* at constant temperatures (data from Suenaga 1963).



9. Survival rate in the nymphal stage of *N. lugens* at constant temperatures (data from Suenaga 1963).



10. Days required for completion of embryonic development of *N*. *lugens* at constant temperatures (data from Suenaga 1963).



11. Days required for completion of postembryonic development of *N. lugens* at constant temperatures (data from Suenaga 1963).



12. Preoviposition period of *N. lugens* on rice seedlings (Norin 18) at constant temperatures (data from Mochida 1964a).

3. Females were kept at 28° C for 24 hours after emergence, then at 20° C constant.

4. Females were kept at 20°C continuously after emergence.

The oviposition rates were the highest in the first group and lowest in the fourth. Those in the second and the third groups were intermediate and about constant throughout the oviposition period (40 to 50 days). This means that temperatures shortly after emergence affect macropterous females in oviposition for long periods (Mochida 1964a).

The temperature conditions not only during the adult stage but during the nymphal stage affect adult longevity, oviposition rate, and preoviposition period in macropterous females. It is difficult to determine which temperature

conditions are best suited to population growth of *N. lugens*, but day temperatures of about 28 to 30° C and somewhat lower night temperatures may be suitable for producing large number of adults in the field.

When females with both wing-forms are kept at constant temperatures, their ovarioles do not develop below 17 or 18° C. When such females are kept daily at 25°C for several hours in several days, they start to produce eggs below 17 or 18° C (Mochida, unpubl.). This suggests that egg-formation proceeds in response to hormonal activities at above 17 or 18° C.

Appearance of wing-forms

N. lugens has two wing-forms (Fig. 13). The fact that in delphacids higher population densities during the nymphal stage increase the relative number of macropterous adults was found first by Murata (1930) in *L. striatellus*. According to Kisimoto (1956a,b), relative numbers of the macropterous form of the female of *N. lugens* increased with increases in population density. However, brachypterous males did not appear at the lowest density, but were more numerous at middle densities, decreasing again with density increase. Kisimoto (1957), renewing the food plant at different intervals and using several chemicals, found that deterioration in quality and quantity of food accelerated the increase in relative numbers of the macropterous insects of both sexes. The effect of crowding with feeding unchanged is considered to be a group effect or mutual stimulus. Crowding of nymphs is known to affect the adult wing-forms in



13. Wings of macropterous (M) and brachypterous (B) adults of N. lugens.

N. lugens (Miyake et al 1951; Johno 1963), as it does in *Javesella pellucida* (F.) (Mochida 1973a). Kisimoto (1957) noted that in *N. lugens* the nymphal period is shorter for the brachypterous form than for the macropterous in both sexes, and that even at high densities, the nymphal period of the brachypterous insect is fairly constant, whereas that of the macropterous insect is lengthened by greater density. A strain producing abundant brachypterous adults was unintentionally selected from the offspring of brachypterous females for many generations (Mochida 1975).

Reproduction

Reproductive organs. Spermatogenesis and oögenesis have been studied by Suenaga (1963). Rudimentary reproductive organs are found in first-instar nymphs. The spermatogonia and the spermatocytes in early stages are present in the middle of the first-instar span. The maturation division of spermatogenesis starts between the end of the third-instar and the early fifth-instar period. The spermatozoa are seen at the bottom of the testicular tubules in the fifth-instar. Because the *N. lugens* female has acrotrophic ovarioles, oögenesis advances rapidly after emergence, as in other delphacids (Mochida 1970, 1973a).

The male reproductive organs consist of two testes, six vasa efferentia, two vasa deferentia, two accessory glands, and a median ejaculatory duct (Fig. 14). Each testis is composed of three lemon-shaped testicular tubules.

The essential parts of the female reproductive organs are a pair of ovaries, a pair of lateral oviducts, a median oviduct, spermatheca, and vagina (Fig. 15). An ovary is made up of a number of ovarioles. An ovariole is made up of a



14. The internal reproductive organs of *N. lugens* (male adult). a = accessory gland; ae = aedeagus; e = ejaculatory duct; t = testicular tubule; vd = vas deferens; ve = vas efferens.



15. The internal reproductive organs of *N*. *lugens* (female adult). b = bursa copulatrix; lo = lateral oviduct; mo = median oviduct; ov = ovary; p = pouched gland; s = spermatheca.

terminal filament, germarium, vitellarium, and ovariole pedicel (Fig. 16). Suenaga (1963) calculated theoretically that the maximum total number of oöcytes produced within a female body was 1,728 to 1,984. He observed that one female produced 1,474 eggs (see Table 4).

Copulation, egg-formation, and egg-deposition. Adult males on rice plants. before copulation, are attracted by the abdominal vibration of females even from a distance of about 80 cm (Ichikawa and Ishii 1974; Ichikawa et al 1975; lchikawa 1976). For 24 hours after emergence males cannot copulate. Their ability to copulate increases up to 5 days after emergence, then decreases (Takeda 1974). A male can copulate at most with nine females for 24 hours; a female can copulate two or more times during her life time (Mochida, unpubl.). Egg-formation is not related to copulation, but discharge of fully grown eggs from the vitellarium of the ovariole is related to copulation, as in the delphacid J. pellucida (Mochida, 1970, 1973a). The number of eggs laid by females during their life spans ranges between 0 and 1,474 (Table 4). The number of eggs laid is correlated to life span and ovipositional period, as mentioned in the section on effect of temperature. Although there are many data from several authors, because of large individual variations it seems difficult to decide whether females of one wing-form produce more eggs than females of the other. However, brachypterous females start to oviposit earlier than macropterous females in cool environments. The preoviposition period averages 3 or 4 days for brachypterous females but 3 to 10 days for macropterous ones



16. Longitudinal section of the ovarioles of *N. lugens* (macropterous female). A; female within 4 h after emergence; B; 7-day-old female; C; 7-day-old female (part of the vitellarium); D; 20-day-old female. a = arrested cell; ep = epithelial plug; es = epithelial sheath; f = f_ully developed egg; fc = follicular cell; g = germarium; gv = germinal vesicle; ip = interfollicular plug; l = last remains of corpus luteum; m = mycetocyte; nc = nutritive cord; o = growing oöcyte without yolk; oy = oöcyte with yolk; pd = pedicel; po = primary oöcyte; pt = prefollicular tissue; l = basal part of the terminal filament; fc = trophocyte; tr = trophic core; tt = trophic tissue; v = vitellarium (Mochida 1970).

at constant temperatures of 20 to 33°C. Egg-formation is interrupted when fifth-instar female nymphs are irradiated at 15 to 20 krad by Cobalt 60 (Mochida 1973b).

Dispersal

Nymphs and brachypterous adults move by walking and hopping; macropterous adults move by flying, walking, and hopping. First- to fifth-instar nymphs can move 4.8, 10.0, 18.5, 20.7, and 21.1 cm, respectively, at 16°C by hopping (Mochida 1970). The migration and flight of macropterous adults are influenced greatly by their age, sex, and climatic conditions. Macropterous adults take off for flight around sunrise and sunset. Light intensity adequate for takeoff flight is about I to 200 lux. The frequencies of flight activity of *N. lugens* form a bimodal crepuscular curve at times in the temperate zone when low temperatures may suppress sunset flight to produce a unimodal pattern. The low temperature threshold for takeoff is about 17°C. Flight behavior or takeoff is suppressed by winds more than 11 km/hour (Ohkubo and Kisimoto 1971). Flight activity seems to continue under conditions of low temperature, high humidity, and weak wind (Ohkubo 1973). MacQuillan (1975) observed in the tropics that the diurnal flight activity of *N. lugens* has a unimodal crepuscular pattern.

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